



Carbon sequestration and methane emissions along a microtopographic gradient in a tropical Andean peatland

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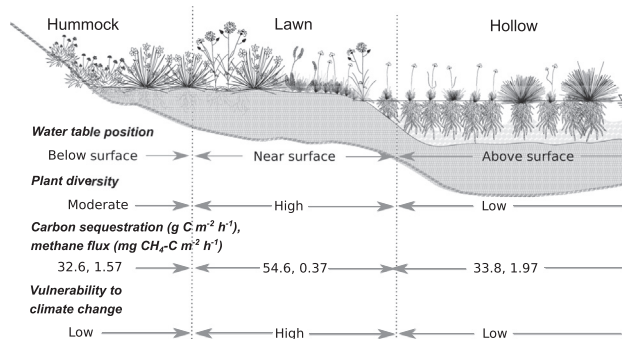
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HIGHLIGHTS

- Methane fluxes and carbon storage were measured along a water table gradient.
- Near-surface water table and plant diversity maximize carbon sequestration.
- Near-surface water table and plant diversity minimize methane emissions.
- Climate change will likely increase vulnerability of climate-regulating service.

GRAPHICAL ABSTRACT



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ABSTRACT

Tropical alpine peatlands are among the least studied wetlands types on earth. Their important ecosystem services at local and regional scope are currently threatened by climate and land use changes. Recent studies in these ecosystems suggest their importance to the provision of climate regulation services, prompting a better understanding of the underlying functions and their variability at ecosystem scales. The objective of this study is to determine the variability of methane (CH₄) fluxes and carbon (C) sequestration within a tropical alpine peatland in three locations along a microtopographic gradient and its associated plant diversity. These locations accounted for: 1) hummocks, found mostly near the edge of the peat with a water table below the soil surface, 2) lawns, in the transition zone, with a water-table near the soil surface, and 3) hollows, permanently flooded with a water table above the soil surface, composed of small patches of open water intermingled with unconsolidated hummocks that surface the water level. Results indicate that CH₄ flux is lowest in the lawns, while C sequestration is highest. Conversely, the hummock and hollow have higher CH₄ flux and lower C sequestration. In addition, plant diversity in the lawns is higher than in the hummock and hollow location. Drier conditions brought by current climate change in the northern Andes are expected to lower the water tables in the peatland. This change is expected to drive a change in CH₄ flux and C sequestration at the lawns, currently dominating the peatland, towards values more similar to those measured in the hummocks. This decrease may also represent a change towards the lower plant diversity that characterized the hummock. Such changes will reduce the ratio of C sequestration:CH₄ flux signifying the reduction of resilience and increment of vulnerability of the climate-regulating service to further perturbations.

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1. Introduction

Peatlands accumulate significant amounts of carbon (C) in their anaerobic soils as partially degraded organic matter or peat. This accumulation results primarily from impaired decomposition of organic matter due to the biochemical inhibition of enzymatic activity (Freeman et al., 2004), and due to organometallic complexation (Wang et al., 2017). This process of organic matter accumulation in the soil, known as C sequestration, constitutes an important climate-regulating function, by retaining C that otherwise will be released back as CO₂, the major greenhouse gas (GHG). However, the anaerobic conditions that allow the accumulation of C lead to production and consequent release of methane (CH₄), which is also a potent GHG.

Both, C sequestration and CH₄ emissions are highly dependent on the hydrologic dynamics of peatlands and the plant communities present on them. On the one hand, water level controls the degree of saturation in the soil that drives the anaerobic conditions, which trigger the biochemical inhibition of peat (Freeman et al., 2004) and the production of CH₄ (Bridgham et al., 2013). On the other hand, plants as the major source of organic matter, control C sequestration and CH₄ production by determining the quantity and quality of degradable and recalcitrant organic matter and the nutrients used by microbes decomposing the peat (de Graaff et al., 2014). Root exudates are also significant sources of dissolved organic C (DOC), which is used by decomposing microorganisms as energy source (Laanbroek, 2010). Moreover, plants also play an important role as one of the main pathways for methane transport to the atmosphere through their vascular tissues (Dorodnikov et al., 2011).

Because of the dual effect on the radiative forcing of peatlands by sequestering CO₂ (negative radiative forcing) and emitting CH₄ (positive radiative forcing), assessing the climatic role of peatlands (i.e. cooling vs warming) and its linked climate-regulating ecosystem service, can only be done by accounting simultaneously for these two coupled functions (Neubauer and Megonigal, 2015). This can be done through dynamic modeling approaches (e.g. Mitsch et al., 2013; Neubauer, 2014). However, in practice, this can simply be assessed with the ratio of C sequestration to CH₄ emissions, which represents the ratio between contributing negative and positive radiative forcing (e.g. Neubauer and Megonigal, 2015). The lower the ratio, the higher the potential negative impacts due to high CH₄ emissions vs. low C sequestration, and thus the lower the offer of climate-regulating service.

Climate regulating functions in northern boreal and sub-arctic peatlands and their role in climate regulation has been extensively documented (Roulet, 2000; Frolking et al., 2006; Frolking and Roulet, 2007; Roulet et al., 2007). In the tropics, most of the studies have focused on lowland zones, with extensive areas of peatlands in Indonesia (Page et al., 2004; Hadi et al., 2005; Jaenicke et al., 2008; Page et al., 2011) and in the Amazon (Lähteenoja et al., 2009; Lähteenoja et al., 2011; Gumbrecht et al., 2017) accounting for the majority of studies, while considerably less attention has been paid to peatlands in other tropical zones, especially in the mountain ranges.

The tropical Andes comprises a region of approximately 490,000 km², stretching from western Bolivia and southern Peru in the south, to Venezuela in the north (Josse et al., 2013). Alpine ecosystems, occurring along this range can be dividing in two biomes: the *páramo* in the humid tropics, and the *puna*, in the highlands of Peru and Bolivia, characterized by drier conditions than those in the *páramo* (Buytaert et al., 2011). The *páramo* region covers an estimated area of 36,000 km² (Buytaert et al., 2011) in a discontinuous belt from Venezuela in the north, to Ecuador in the south, at elevations ranging from 3200 to 4700 m.a.s.l. (Lauer, 1981). The *páramo* ecosystems consist of an assemblage of small lakes and peatlands, intermingled with grass and shrublands, and sparse forest patches (Buytaert et al., 2006). Water regulation in these ecosystems is key to supply fresh water for human consumption, hydropower generation, and agricultural and industrial activities, providing more than half of the demand of water to

downstream regions, benefiting several millions of people in the region (Buytaert et al., 2006; Buytaert and De Bièvre, 2012; Mosquera et al., 2015).

Nonetheless, *páramo* provision of ecosystem services is highly fragile to human perturbation and climate change. Land-use changes for mining and agricultural activities shift hydrological regimes and ecosystem functioning and composition (Buytaert et al., 2007; Robineau et al., 2010; Urbina and Benavides, 2015; Ochoa-Tocachi et al., 2016; Sánchez et al., 2017; Pérez-Escobar et al., 2018). Increasing temperature and changes to precipitation patterns are having and expected to have further major impacts on *páramo* hydrology and associated ecosystem functions (Ruiz et al., 2008; Poveda et al., 2011). Under this context, sustainable management and associated practices, such as conservation and restoration of *páramo* ecosystems, have become an increasing priority (e.g., Robineau et al., 2010). However, the lack of knowledge of other important ecosystem services beyond water provisioning, such as climate regulation, represents a challenge for designing multi-target conservation and restoration initiatives to protect the remaining *páramo* sites and re-establish ecosystem functioning of degraded sites (Farley et al., 2011; Villa and Bernal, 2018).

While the tropical Andean peatlands do not cover extensive areas as its counterparts in boreal and subarctic regions or in the tropical lowlands, they are abundant (Hribljan et al., 2017) and likely important in the cycling of C from local to regional scales. Recent studies have shown that they have relatively faster C sequestration and larger C stocks than other peat-accumulating ecosystems in other regions and climates (Chimner and Karberg, 2008; Benavides, 2014; Hribljan et al., 2016), and with lower CH₄ fluxes (Teh et al., 2013; Sánchez et al., 2017; Veber et al., 2018). However, to date, no studies have evaluated C sequestration and CH₄ fluxes in the same *páramo* site, preventing a comprehensive assessment of the potential climate-regulating service offered by these ecosystems. Moreover, it is not clear how C sequestration and CH₄ fluxes relate to hydrologic conditions and other attributes of the ecosystem. This relationship is of interest for the design of restoration projects aiming to re-establish these functions, and of ecosystem management activities seeking to maximize co-benefits and reduce trade-offs between ecosystem services (Rodríguez et al., 2006; Goldstein et al., 2012; Smith et al., 2012).

In this study, we evaluated the variability of C sequestration and methane CH₄ fluxes within a tropical Andean peatland of the *páramo* in three locations along a microtopographic gradient and its associated plant diversity. We used these results to assess the potential climate regulating service offered by this peatland and its vulnerability to current changing trends in temperature and precipitation observed in this part of the northern Andean mountain range.

2. Methods

2.1. Study site

This study was conducted in *El Morro*, a 40-ha tropical alpine peatland in the *Páramo* of Belmira in the northern Andean Mountains, central branch (*Cordillera Central*) in Colombia, at 3200 m.a.s.l. (06° 40' 54" N, 75° 40' 37.6" W) (Fig. 1A). *El Morro* is situated in a mountain range on a valley that was originated from fluvioglacial deposition during the Holocene (Arias, 1995). The peatland is primarily rainwater fed, with a total drainage basin area of 145 ha. Across the longitudinal stretch of the valley, the site features a distinct transversal microtopographic gradient from hammock and drier portions of peat with water tables below the soil surface near the margins, to hollow, permanently flooded portions towards the middle (Fig. 1B). Most of the peatland area is composed of lawns at transitional elevations with water tables near the soil surface. Prior to 1997 the fringes of the peatland were used for extensive cattle ranching (Villa, 2017). The permanently flooded hollow act as headwaters for two first-order streams that run from each end of the valley and are part of an important local

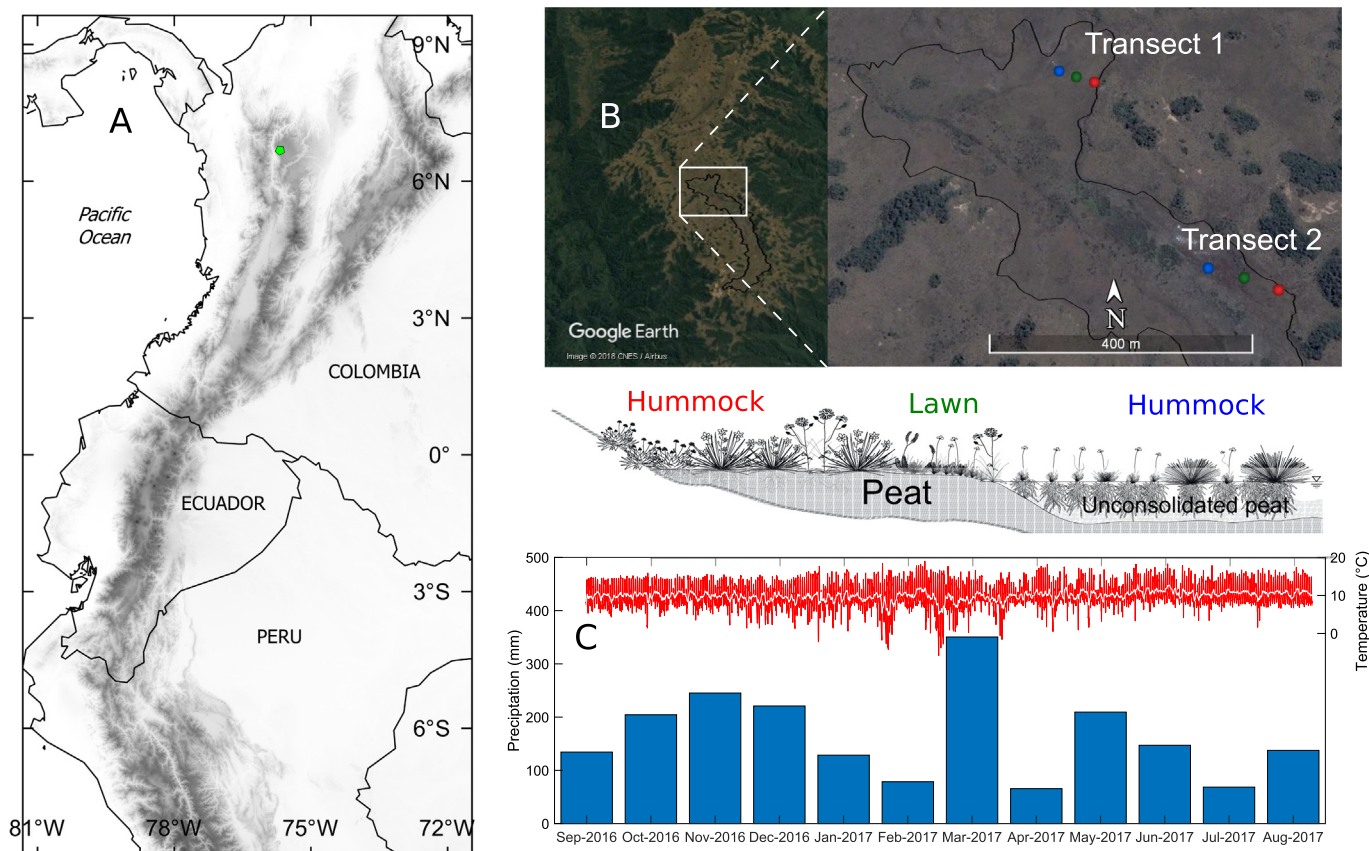


Fig. 1. Study site. A) Shows the general location on the study site (green) in the northern Andes mountain range. B) Study site showing the two transects and sampling locations along the microtopographic gradient, hummock (red), lawn (green) and hollow (blue). C) Monthly precipitation and hourly temperature records for the sampling period (09/01/2016 to 08/10/2017). Precipitation data is from a nearby weather station operated by IDEAM Colombia (station No. 27010) located at 3.3 km from the study site. Temperature was measured in-situ with a weather station.

watershed, which provides drinking water to more than million people and is also used for hydropower generation (Corporación Autónoma Regional del Centro de Antioquia - Corantioquia, 2005).

The study period extended nearly a year from 09/01/2016 to 08/10/2017. Mean \pm SD temperature ($^{\circ}\text{C}$) during this period was 9.9 ± 3.2 and showed no seasonal variation. Maximum and minimum hourly temperatures were observed towards the end of February 2017, roughly around the middle of the sampling period (19°C and -5.8°C , respectively) (Fig. 1C). Cumulative precipitation during the study period was 1990 mm. Monthly distribution of precipitation shows two high-rain seasons per year, common to this part of the Andes, due to the double passage of the intertropical convergence zone (Sep–Nov and Apr–May), with an unusual peak in rainfall observed in March 2017 (Fig. 1C).

2.2. Water table depths measurements

Two water-table depth transects were established along straight lines in the northern end of the peatland (namely, transects 1 and 2, see Fig. 1), each extending along a ground elevation gradient, from the driest (hummock), easily distinguishable by the presence of dwarf shrubs, through the intermediate lawn, to the wettest (hollow) sections of the peatland. The hollow areas are partially filled pools with discontinuous unconsolidated peat profiles, featuring sparse surfacing vegetation. At each transect, three measurement points were set at hummock, lawn and hollow locations. Water table at each hollow location was measured continuously with pressure-transducer water-level loggers during the study period. For the rest of the locations, 16 discrete measurements were obtained manually at different times using limnometers installed on piezometers. The continuous measurements

from hollow locations were aligned with these discrete measurements to recreate the water-table time series at each location for the study period. All water tables were measured relative to the peat surface at each location.

2.3. Plant community characteristics measurements

Sampling to determine plant cover, frequency and composition were conducted using the Point-Intercept, Grid-Frame method (Bonham, 2013). Accordingly, $20\text{ m} \times 20\text{ m}$ plots were established at each location. At each plot, 5 east-west transects, were marked with rope, 5 m apart. Along these transects, a $27\text{ cm} \times 27\text{ cm}$ sampling frame was deployed every 1 m. The frame had 4 vertical thin wood sticks at each corner that were used to record plant hits. We recorded the species for every plant that touched the sticks, and when plants were not present, we recorded the hit as open water. Plant Diversity within each plot was then measured using the Shannon-Wiener index (H) as $-\sum p_i \ln p_i$, where p_i is the relative abundance of the i th species (Fedor and Spellerberg, 2013). Bray-Curtis dissimilarity index was used to evaluate the difference in plant species between the two transects (Bray and Curtis, 1957).

2.4. Methane fluxes

CH_4 sampling was conducted using static chambers (Livingston and Hutchinson, 1995). At the hummock and lawn locations, these chambers consisted of 30.5 L chambers made of transparent polypropylene squared frames inserted 10 cm in the soils and surfacing another 10 cm. At each sampling, removable chamber tops with foamy rims were fitted on these frames and mechanically sealed with plastic

grabs. Chamber tops were equipped with plastic tubing for pressure relief, a rubber sampling port, a digital thermometer to measure temperature inside the chambers and a small 12 V fan for air mixing inside the chamber during chamber deployment. Chambers in the deep locations consisted of a 20 L modified floating version of the above. We used 3 chamber replicates at each transect location.

Three chambers (replicates) were deployed at each location 8 times during the study period, with an approximate frequency of 45 days. Deployments took place during daytime, between 9 am and 4 pm. Two additional nighttime deployments occurred during a high- and a low-rain season (i.e., May and August, respectively) between 8 pm and 11 pm. Chamber deployment at each sampling date and location was performed for 25 min. During this time, 15 mL subsamples of gas were collected with a syringe at 5 minute intervals and placed in pre-evacuated 10 mL vials sealed with gray butyl septum. The temperature inside the chamber was recorded at sample collection times, in addition to soil temperature for the top 10 cm. For the initial interval (i.e., time zero), samples were collected in the open air above the chamber frames just before the top assemblage to avoid possible disturbance during chamber enclosure.

CH₄ concentration in each sample was determined by flame ionization detection in a gas chromatograph coupled with a headspace autosampler. Volume concentrations (mL CH₄ L⁻¹) from chromatographic analysis were converted into mass/volume concentration (mg CH₄-C m⁻³), using the ideal gas law following (Holland et al., 1999). For each chamber run, fluxes were calculated as the product of the slope of the linear regression of mass/volume concentrations versus time (mg CH₄-C m⁻² min⁻¹) and the volume of the chamber, divided by the surface area covered by the chamber. These fluxes were later transformed into hourly fluxes (mg CH₄-C m⁻² h⁻¹) and are presented in these units through the paper unless noted otherwise. Only significant regressions at a 0.1 significance level were assumed to represent non-zero fluxes. Of 180 chamber runs over the course of the study, 89 runs showed flux. Zero flux was assumed when most data were below detection limit or had regressions with non-significant slopes.

2.5. Carbon sequestration

Undisturbed soil core samples were collected using a Watermark™ universal core-head sediment sampler (Aquatic Research Instruments, Hope, ID, USA) equipped with a 6.5 cm I.D. polycarbonate barrel. One core at least 40 cm long was collected at each plot from transects 1 and 2. At the hollow locations, cores were collected at the bottom of the pools on consolidated peat. Cores were sectioned in 2-cm depth increments in the field, bagged and transported to the laboratory for further processing. Samples were oven-dried at 55 °C for 48 h, and dry weight was recorded. Then, samples were grinded and homogenized to 2-mm particle size using mortar and pestle. Distinguishable roots or other plant materials were removed during this process. Samples were re-dried at 55 °C for another 12 h to remove any moisture regained during homogenization. Total carbon (TC%) for each depth increment was measured from 5 subsamples (~3.5 mg) of dry soil through dry combustion at 1080 °C, in a Micro Cube elemental analyzer with an infrared detector (Elementar Analysensysteme GmbH, Hanau, Germany). We reported soil TC concentrations in g C kg⁻¹.

Core depth chronologies to determine accretion rates were determined with ²¹⁰Pb dating of the top 15 depth increments (i.e., 0–30 cm) using the constant-rate-of-supply (CRS) model (Appleby and Oldfield, 1978). We then integrated the TC of the depth increments down to the depth of the oldest dated increment. Finally, C sequestration (g C m⁻² yr⁻¹) was calculated by dividing this integrated TC concentration by the area of the core and the number of years from the peat surface to the date of the deepest sample. Similarly, we integrated the dry weight to estimate mass accretion rates (g m⁻² yr⁻¹) (e.g. Villa and Mitsch, 2015; Villa and Bernal, 2018).

2.6. Data analysis

As explained above, we sampled along 2 transects and 3 locations (hummock, lawn and hollow) per transect. Soil temperatures during sampling among these locations were compared using a one-way ANOVA test. We treated the three chambers that were deployed at the same date and location as replicates. Non-parametric Wilcoxon signed-rank was used to test the significance of differences in median CH₄ fluxes between samples at each location, and between daytime and nighttime samples. Similarly, Wilcoxon signed-rank was used to test differences in bulk densities and C concentrations between different depths in the soil cores down to the depth that was used to calculate C sequestration. Mann-Whitney *U* test was used to test differences in annual-averaged site's CH₄ fluxes, bulk densities, and C concentrations between same locations at different transects. We used Spearman's Rank Correlation Coefficient to evaluate the correlation between CH₄ flux and soil temperature and between CH₄ flux and water levels at each location. The significance of these correlations was determined using a generalized linear model with Cox-Hazard distribution nested by site. Normality of the datasets was tested using Shapiro-Wilk *W* test. All statistical analyses were run in Matlab R2018a, except the Pearson's correlations that were performed using JMP Pro13.

3. Results

3.1. Environmental conditions - water table and vegetation diversity across the transects

Water-table depth response to single precipitation events was observed in all three locations, while monthly variations did not present distinct seasonal trends except in the hummock location in transect 2 (Fig. 2). At this location, water-table depth dropped considerably when precipitation receded after the Sep–Nov rainy season. Observed water-table depths for all locations are shown in Table 1.

In total, 29 species were identified in the different locations, 24 in transect 1 and 25 in transect 2. Bray-Curtis dissimilarity between the two transects was 26%. Relative abundance showed distinctive patterns of co-dominance along transects (Fig. 3). For example, plants such as *Xyris subulata* and *Sphagnum rubellum* were more abundant towards the wetter locations, while the abundance of *Paepalantus columbiensis* or *Orthrosanthus* sp. was higher in dryer locations. Shannon's diversity index was higher in lawn locations and lower in the hollow locations (Table 2).

3.2. Methane fluxes

Methane fluxes were similar among sampling dates for each location throughout the study period (hummock: $\chi^2(7, N = 48) = 9.76, p = 0.203$; lawn: $\chi^2(7, N = 48) = 8.63, p = 0.28$ and hollow: $\chi^2(7, N = 48) = 4.41, p = 0.731$) and did not show a discernible seasonal pattern (Fig. 2). The soil temperature during CH₄ sampling was similar between locations ($F(2, 57) = 2.77, p = 0.3$). Mean \pm SD soil temperature was 14 ± 1 in hummock, 13.9 ± 1 in lawn, and 14.1 ± 1 in hollow. CH₄ fluxes within each location were correlated with soil temperature only in the lawn, and were correlated with water-table depth only in the hollow (Table 3). All other correlations between flux and water-table depth and between flux and soil temperature at different locations, were not significant. Additionally, the differences between nighttime and daytime fluxes were not significant during neither the high- nor the low rain-seasons ($\chi^2(3, N = 6) = 2.83, p = 0.419$). The overall nighttime mean \pm SD during the May and August samplings were 2.94 ± 6.64 and 4.08 ± 9.31 mg CH₄-C m⁻² h⁻¹, respectively.

Observed CH₄ fluxes per locations for the study period are shown in Fig. 4A. Fluxes in the hummock (1.57 mg CH₄-C m⁻² h⁻¹) and hollow (1.97 mg CH₄-C m⁻² h⁻¹) were similar (Mann-Whitney $U_{38} = 197, Z = -0.081, p = 0.947$) and significantly higher than the flux

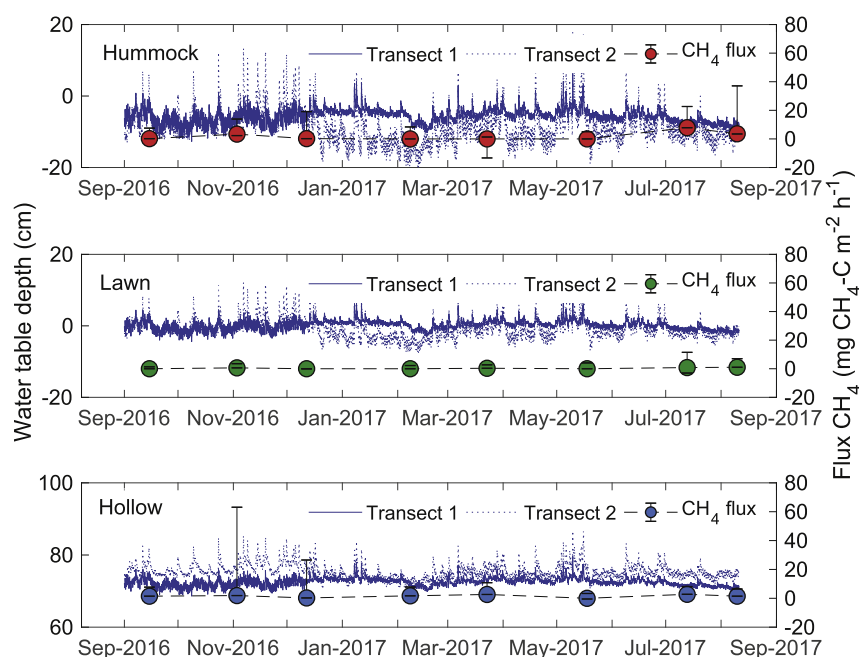


Fig. 2. Water table depth during the study period (bold and dashed blue lines) and CH_4 fluxes for hummock, lawn and hollow locations (red, green and blue circles respectively). Error bars in CH_4 fluxes represent the 90th and 10th percentiles. CH_4 fluxes were similar for each location throughout the study period.

in the lawn ($0.37 \text{ mg CH}_4\text{-C m}^{-2} \text{ h}^{-1}$, Mann-Whitney $U_{38} = 121$, $Z = -2.149$, $p = 0.033$, Mann-Whitney $U_{38} = 114.5$, $Z = -2.331$, $p = 0.02$, respectively). The low CH_4 flux in lawns corresponded with the combination of high diversity and near-soil-surface water-table depth. In contrast, higher fluxes from both the hummocks and the hollows corresponded with intermediate to low vegetation diversity values, and extreme water-table depths, either below the soil surface (in the hummocks) or well above it (in the hollows) (Fig. 5A).

3.3. Carbon sequestration

C sequestration ranged between $31 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the hollow location of transect 1 to $63.3 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the lawn location of transect 2 (Table 4). C sequestration had the highest mean values at the lawns (Fig. 4B). Average ^{210}Pb background concentrations was 0.034 Bq g^{-1} . This concentration was found at different depths along the transects. Consequently, the depth of the dated peat profile at each location was also different. The deepest increment dated was at 26 cm in the hummock of transect 2 which was also the older increment dated (217 yr), while the shallowest and more recent was at the 10 cm in the hollow of transect 1 (87 yr).

Bulk densities corresponding to the depth from the surface to the deepest dated increment were similar between cores in the same locations in the transects, however they were lower in hummocks than in lawns (Table 4). C concentration for these same depths were different in hummocks and lawns, being higher in cores collected in transect 2,

and were similar in the cores collected in hollows. There was no difference in C concentration between locations (Table 4).

4. Discussion

4.1. Water table and vegetation diversity across the transects

The northern Andean ecosystems are highly dependent on precipitation (Ruiz et al., 2008). Precipitation is by far the major hydrological process driving the water table dynamics of páramo peatlands, although subsurface flow may also be of relative importance, depending on the size of the draining basin, and connectivity with underground sources higher in the landscape (Valencia-Leguiamón, 2016). Water-table response to variations in precipitation is further modulated by the water storage capacity of the peat. Under saturated conditions, peat can retain up to 90–98% of water by mass depending on its bulk density, which in turn depends on peat porosity (Holden, 2005a). On the lawns and hollows, water tables were maintained close or above the peat surface resulting in saturated or near saturated conditions. At saturation, water movement is restricted to the saturated hydraulic conductivity of the peat (Evans et al., 1999). However, below saturation, as was the case during most of the time at the top of the peat profile in hummock locations, hydraulic conductivity is higher, and water can move rapidly through the macropores in the peat (Holden, 2005b), explaining the more accentuated responses in the water tables recorded at these locations.

As expected, plant relative abundance varied along the microtopographic gradient in response to the water table. This variation featured a gradual replacement of functional groups from vascular plants adapted to more dryer conditions (i.e. shrubs and grasses) to other groups adapted to wetter conditions (i.e. mosses). A similar replacement was also noted in a study contrasting undisturbed and drained tropical Andean peatlands (Benavides, 2014), and in mesocosm-scale manipulations of northern peatlands (Weltzin et al., 2000; Weltzin et al., 2003; Potvin et al., 2015). Similarly, plant diversity changed along the water-table depth gradient. Lower diversity in

Table 1
Mean \pm SD water table levels (cm) during the study period (09/01/2016 to 08/10/2017).

Location	Transect 1	Transect 2
Hummock	-5.6 ± 2.1	-8.4 ± 4.9
Lawn	0.2 ± 1.4	0.7 ± 2.9
Hollow	72.5 ± 2.2	75.5 ± 2.2

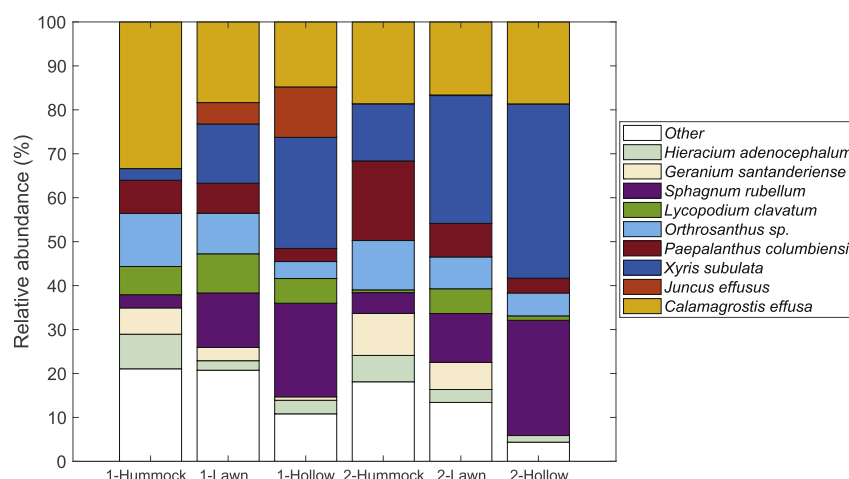


Fig. 3. Relative abundance of plant species along the two transects evaluated. “Other” accounts for species with abundances lower than 5%.

hummocks was attributed to enhanced habitat condition for species less adapted to flooded conditions (Cao et al., 2017). Conversely, low diversity in the hollows was explained by the dominance of flood tolerant species (Bakker et al., 2007). In addition, species such as *S. rubellum* usually dominant in wet peatland environments have been known to further inhibit vascular plant growth through the release to the environment of highly acidic metabolites (Verhoeven and Liefveld, 1997). At the intermediate water-table depths of the lawn locations, diversity was relatively higher. Plant diversity at this transitional water-table depth location can be promoted by the constantly changing aerobic-anaerobic environment brought by fluctuations of the water table near the surface of the peat, which can increase nutrient availability (Reddy and Patrick Jr., 1975; Richardson, 1985), and allow for species competition, thus reducing species dominance (Budelsky and Galatowitsh, 2000). This finding is consistent with patterns of Bryophyte diversity in Peatlands of Canada (Vitt et al., 1995) and natural (Bruland and Richardson, 2005) and constructed (Vivian-Smith, 1997) temperate mineral-soil freshwater wetlands.

4.2. Methane fluxes

Water-table level and temperature are known to be the major physical controls of methanogenesis in peatlands at large scales as inferred from top-down modeling, with water tables being more important in tropical areas due to a relatively higher variation in water tables and the lack of marked seasonal variations in temperature in these regions (Bloom et al., 2010). Our results partially support this at the ecosystem-scale. These controls did not show a clear pattern nor were consistent along the microtopographic gradient. Temperature only correlated with CH_4 fluxes in the lawn, the location with the lowest fluxes. This correlation was weak and negative (Table 3) suggesting that

instead of promoting methanogenesis, temperature may be promoting methanotrophy (Le Mer and Roger, 2001), thus reducing CH_4 fluxes. This process is poorly understood in tropical Andean peatlands. Additionally, the correlation between CH_4 fluxes and the water-table levels was high and positive but only significant in the hollows, suggesting that when the water-table is at or below the peat surface other controlling factors of CH_4 fluxes at the ecosystem scale becomes more relevant. More field efforts should address these knowledge gaps to advance on the development of models that could represent C dynamics in these ecosystems and their integration into global models (Melton et al., 2012).

Median CH_4 flux in lawns during the study period ($0.37 \text{ mg CH}_4\text{-C m}^{-2} \text{ h}^{-1}$) was at the lower range of reported values in other studies in tropical Andean peatlands. For example, Teh et al. (2013) found variations between dry and wet seasons in the puna, from 0.04 to $0.77 \text{ mg CH}_4\text{-C m}^{-2} \text{ h}^{-1}$. In an Ecuadorian páramo, Sánchez et al. (2017) compared fluxes from shrub and grass-dominated portions of the peat (lawns) with hummocks consisting of cushion plants. They found a mean value of $0.79 \text{ mg CH}_4\text{-C m}^{-2} \text{ h}^{-1}$ and no difference between lawns ($0.26 \pm 0.05 \text{ mg CH}_4\text{-C m}^{-2} \text{ h}^{-1}$) and hummocks ($0.42 \pm 0.09 \text{ mg CH}_4\text{-C m}^{-2} \text{ h}^{-1}$). In a previous study in a different location at El Morro Veber et al. (2018) found fluxes ranging from -0 to $2.2 \text{ mg CH}_4\text{-C m}^{-2} \text{ h}^{-1}$.

The hummock and hollow locations showed up to 5-fold stronger median methane flux than the lawn locations (1.57 and $1.97 \text{ CH}_4\text{-C m}^{-2} \text{ h}^{-1}$, respectively). The high methane flux in the drier hummock is not consistent with the classical conceptual model of CH_4 dynamics in peatland ecosystems that predicts lower CH_4 production in drier and more oxic peat profiles (Clymo et al., 1995), and findings at field scale along microtopographic gradients in northern peatlands (Moore and Knowles, 1990; Bubier et al., 1993). Although oxygen levels were not measured in our study, more oxic profiles were likely to dominate the unsaturated portions of the peat above the water table in hummock locations.

Table 2
Shannon's Diversity Index (H) in the different water levels of the two transects evaluated.

	Richness	Shannon's Diversity Index (H)
Transect 1		
Hummock	23	2.37
Lawn	20	2.54
Hollow	17	2.16
Transect 2		
Hummock	22	2.42
Lawn	20	2.78
Hollow	12	1.59

Table 3
Spearman Coefficients (ρ) for the correlations between CH_4 flux and water-table depth, and soil temperature for each location. The significance of these correlations (in italic) were determined using a generalized linear model with Cox-Hazard distribution nested by site (* denotes significant correlations at $\alpha = 0.05$).

Location	Water-table depth	Soil temperature
Hummock	$-0.11, 0.957$	$0.13, 0.260$
Lawn	$-0.13, 0.179$	$-0.15, 0.046^*$
Hollow	$-0.77, 0.002^*$	$-0.04, 0.561$

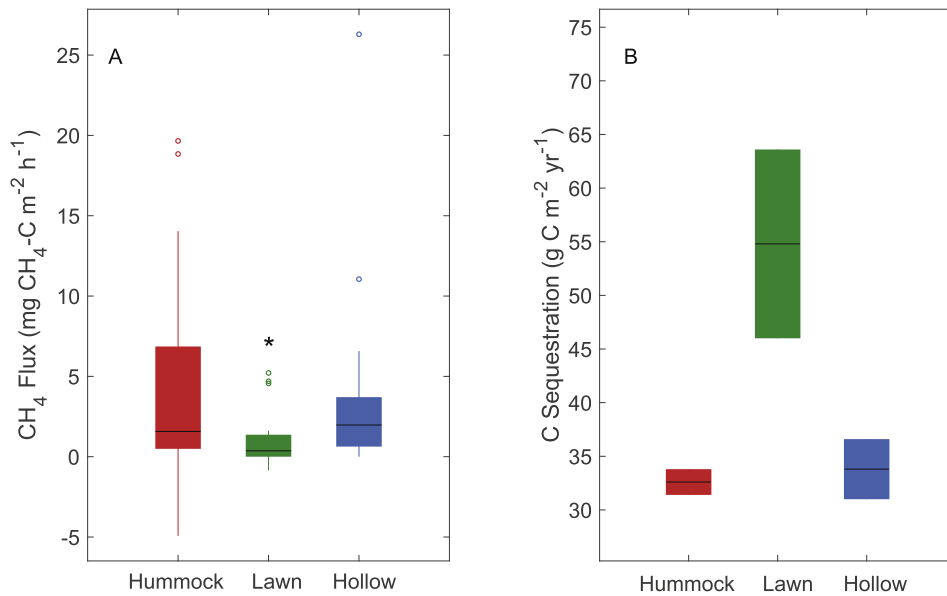


Fig. 4. Boxplots of CH_4 flux (A) and C sequestration (B) by water level class (* denotes statistical different median fluxes). Edges in A boxes' indicate 25th and 75th percentiles and black line the median flux while edges in B indicates the range of values measured and the black line the median = mean values.

Studies conducted in other grass-dominated wetlands in northern latitudes, including peatlands, found increased CH_4 fluxes in locations dominated by graminoids due primarily to plant-mediated transport processes (Turetsky et al., 2014; Davidson et al., 2016; Li et al., 2016). In our site, hummock locations had a higher relative abundance of graminoid vegetation (e.g., *C. effusa* and *P. columbiensis*) than lawns, possibly enhancing CH_4 transport from deeper, anaerobic peat layers. Another potential explanation comes from recent evidence that suggests that CH_4 production is not exclusive of anoxic soils and that CH_4 can be produced in oxic soils due the occurrence of anaerobic microsites (Angle et al., 2017; Yang et al., 2017).

A surprising finding in our study was that CH_4 fluxes were lower at locations with higher plant diversity. To our knowledge, this is the first study to report such a relationship in peatlands or other types of wetlands. Plant diversity can reduce CH_4 emission by increasing below-ground productivity and root exudates which in turn can increase CH_4

oxidation (Le Mer and Roger, 2001). Plant composition can further modulate gas transport processes (Davidson et al., 2016). This has been proved in wetland mesocosms, where CH_4 fluxes were linked with diversity at the functional group-level (Bouchard et al., 2007; Schultz and Pett, 2018). Different plant functional groups have also been linked with microbial community structure differences affecting potential CH_4 production and oxidation (Robroek et al., 2015). However, previous attempts to link CH_4 fluxes with plant diversity in natural wetland ecosystems proved to be inconclusive due to the difficulty to account for the interaction with other environmental factors (Schultz et al., 2011).

Notwithstanding, this finding must be handled with caution, due to important limitations in our study. First, we are reporting diversity at the plot-scale and not to the diversity within the chamber frames that were used for CH_4 flux sampling. Second, diversity was assessed using the Shannon-Wiener index. This index is simple and represents clear advantages for interpretation and comparison of the results. It is frequently used by researchers and practitioners world-wide, despite known inherent statistical and conceptual issues associated with the use of this and other diversity indices (Barrantes and Sandoval, 2009). And third, to fully assess the role of plant diversity in the spatial variation of CH_4 fluxes, studies should include plant attributes such as biomass or leaf area index (not measured in this study), in combination with the knowledge of important species traits such as gas transport (Goud et al., 2017), which is currently missing for páramo peatland plants.

4.3. Carbon sequestration

The C sequestration in the different locations were within the range reported for other tropical Andean peatlands, comprising a range of dry to wet climates (i.e. 9–209 $\text{g C m}^{-2} \text{ yr}^{-1}$, Chimner and Karberg, 2008; Hribljan et al., 2015; Hribljan et al., 2016). Sequestration in lawn locations was above the mean values reported in these studies (i.e., 41.9), while hummock and hollow locations showed lower values. Both, accretion rates and C sequestration in all locations showed values above those estimated for northern peatlands (0.3 and 25.2 $\text{g C m}^{-2} \text{ yr}^{-1}$, respectively) (Tolonen and Turunen, 1996; Trumbore and Harden, 1997; Turunen et al., 2002) and Tibetan alpine peatlands (Chen et al., 2014) (1.3 and 20.4 $\text{g C m}^{-2} \text{ yr}^{-1}$, respectively), providing additional evidence

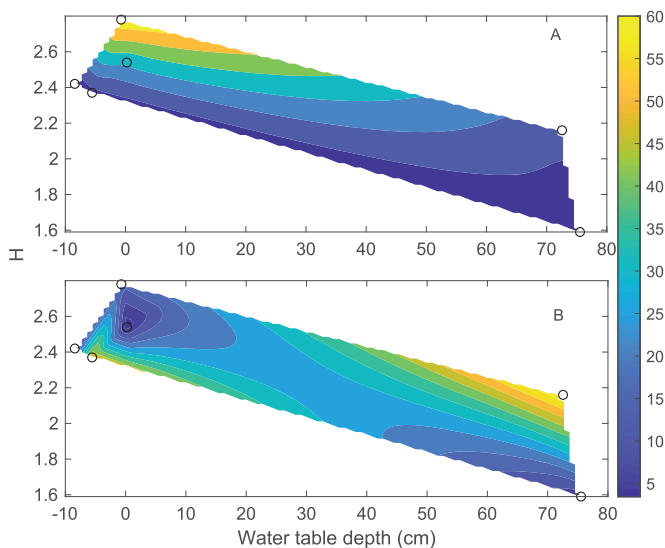


Fig. 5. Mean carbon flux ($\text{g C m}^{-2} \text{ yr}^{-1}$) as a function of water table depth and plant diversity. A) CH_4 flux and B) C sequestration.

Table 4
Depth dated, accretion rate, bulk density, carbon concentration, mass accretion and carbon sequestration for the six cores collected. Mean bulk density and C concentration were calculated from the surface to the deepest dated increment (* denotes higher values on same locations in the transects at $\alpha = 0.05$, while letters represent the difference between locations).

Location/transect	Integrated unsupported ^{210}Pb	Depth dated (age)	Accretion rate	Bulk density (mean \pm SD)	Carbon concentration (mean \pm SD)	Mass accretion	Carbon sequestration
		cm (yr)	mm yr $^{-1}$	g cm $^{-3}$	g C kg $^{-1}$	g m $^{-2}$ yr $^{-1}$	g C m $^{-2}$ yr $^{-1}$
Hummock							
1		24 (157)	1.5	0.07 \pm 0.02 ^a	310.3 \pm 28.7	109.1	33.8
2		26 (217)	1.2	0.07 \pm 0.01 ^a	370.9 \pm 22.7*	116.4	31.4
Lawn							
1		24 (153)	1.6	0.09 \pm 0.03 ^b	310.1 \pm 23.4	144.6	46.0
2		18 (111)	1.6	0.12 \pm 0.03 ^b	354.2 \pm 0.8*	133.8	63.6
Hollow							
1		10 (87)	1.2	0.10 \pm 0.04 ^{ab}	329.5 \pm 15.4	61.3	36.6
2		12 (130)	1.1	0.07 \pm 0.03 ^{ab}	355.9 \pm 35.3	74.3	31.0

that tropical Andean peatlands accumulate larger carbon stocks in relatively shorter periods of time than northern peatlands (Hribljan et al., 2016).

However, we observed high variation of the accumulation rates along the microtopographic gradients. C sequestration was higher at lawn locations, which also have higher plant diversity, while lower values were observed in hummock and hollow locations that exhibited low vegetation diversity (Fig. 5B). Variations in mean water-table level along transects could explain this variation by setting the conditions, dynamics and relative importance of the processes that control organic matter accumulation in peatland ecosystems.

Water-table level in peatlands governs the occurrence (time and space) of anaerobic and aerobic conditions in the peat profile. Anaerobic conditions promote the accumulation of phenolic compounds that prevents organic matter decomposition by inhibiting decomposing enzymatic activity (Freeman et al., 2001; Fenner and Freeman, 2011). Conversely, aerobic conditions increase peat decomposition (Strack and Waddington, 2007). Water-table heterogeneity control the composition of plants communities (Vivian-Smith, 1997) and thus, the quality of organic matter undergoing decomposition. For instance, moss species conspicuous to peatland ecosystems have structural tissues of high recalcitrance that decompose slower than tissues of other peatland vascular species (van Breemen, 1995; Verhoeven and Toth, 1995), and increases phenolic inhibitory effects on decomposition (Jassey et al., 2011).

In addition, heterogeneity in water-table, also regulates plant community productivity. Usually, hummocks and lawns have higher productivity than hollows (Strack and Waddington, 2007). The resulting accumulation of soil organic matter from the balance between decomposition and production further increases water storage capacity by reducing the bulk density, which in turn, raises the water table in a positive feedback that can further slow peat decomposition (Ise et al., 2008).

The net effect of these feedbacks from water-table depth seemed maximal in the lawns, where water tables were near the soil surface most of the time, enhancing of C sequestration. In contrast, in the hummocks, the predominant water tables were below the peat surface, which enabled aerobic decomposition of superficial peat (Wiedermann et al., 2017), likely resulting in a negative effect on organic matter accumulation. Whereas in hollow locations, permanently flooded conditions may have facilitated C loss from unconsolidated peat as dissolved and particulate organic matter to headwater streams (Holden, 2005a), explaining the relative lower C sequestration at this location.

4.4. Implications for management

The ratio of C sequestration to CH₄ flux was highly variable along the microtopographic gradient (Fig. 6). Lawns had ratios up to 28 but also showed high variability with values as low as 4, while hummock and

hollow locations had lower ratios with a narrower variation. Evaluating the potential climatic role that *El Morro* may be playing based on these ratios or other commonly used metrics that compare negative (GHG sink) and positive (GHG source) radiative forcing, such as the Global Warming Potential GWP (e.g., Anderson et al., 2016; Fortuniak et al., 2017), or the Sustained Global Warming Potential SGWP (e.g., Holm et al., 2016) may lead to wrongful conclusions. These metrics evaluate the time-integrated radiative forcing created by a pulse emission of a given component (in this case CH₄), relative to a pulse emission, in the GWP of CO₂. The GWP for a time horizon of a 100 years is 28 (Myhre et al., 2013), and the SGWP is 45 (Neubauer and Megonigal, 2015). In the best-case scenario, the highest range of the ratio in lawns, 28, indicates a neutral source of GHG under GWP and a net sink under SGWP.

However, GWPs were created to compare single-pulse fluxes, which is not ecologically justified in the ecosystem context (Neubauer and Megonigal, 2015). Despite the fact that the SGWP overcame part of this major flaw, it is not retroactive and if used in existing wetland ecosystems, it may be ignoring the C pool already sequestered. Alternatively, based on a dynamic modeling approach, Neubauer (2014) based their evaluation on the switchover times, i.e., the time at which ecosystems switch from net GHG sources to sinks. They found that in freshwater wetlands in mineral soils with C sequestration:CH₄ flux ratios from 0.1 to 25, the switchover time will range between ~60 and 14,000 years. Similarly, Frohling and Roulet (2007) found that during

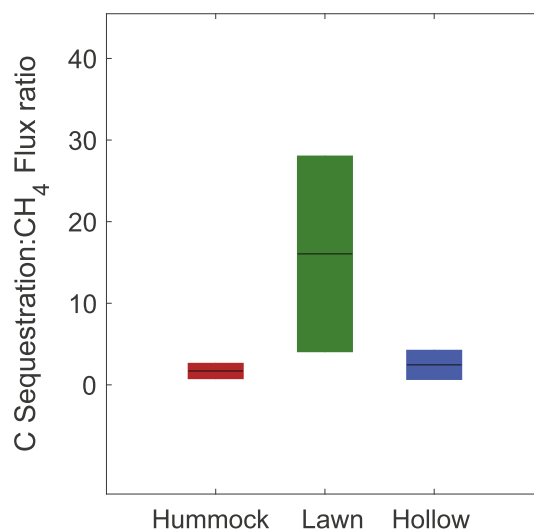


Fig. 6. C Sequestration:CH₄ ratios for the different sampling locations in the transects. Boxes edges represent the range of the ratio for each location and the horizontal line the average ratio.

the past 8000–11,000 years northern peatlands have accumulated a net negative (cooling) radiative effect. Considering these references, and the fact that according to pollen records *El Morro* is at least 11,000 years old (Castañeda-Riascos, 2013), it is probable that this peatland is already a net GHG sink.

We do not advocate the direct use of the C sequestration: CH₄ fluxes ratios to evaluate the climatic role of *El Morro* and assume that it is already providing a climate regulating role as a GHG sink. Instead, we propose to use the C sequestration: CH₄ fluxes ratios to assess the vulnerability of the provision of this service to current trends in climate change in the tropical Andean region. Given that this ratio combines the quantification of both major climate-regulating functions (C sequestration and CH₄ emissions) and structural components (plants mainly) influencing these functions, it is plausible to assume that the ranges of the ratios represent the limits within which, these functions and structure are maintained under natural perturbations. Adopting the classical definition of resilience by Holling (1973), narrower ratios can be interpreted as low resilience while higher ratios as high resilience. The less resilient, the more vulnerable (Gallopín, 2006).

Studies conducted in the northern Andean region indicate rapid climatic changes compared to lowland locations. These changes feature decadal temperature increases of up to 0.7 °C coupled with decreases of relative humidity and reductions in precipitation up to 11% (Ruiz et al., 2008; Ruiz et al., 2012). Under this scenario, it is likely that *El Morro* will experience dryer and warmer conditions to be manifested in lowered water-table tables and increased air and soil temperatures. These expected future conditions may drive a gradual shift in hydrology and plant diversity in the short-term (years to decades), from dominating transition-like lawn conditions to conditions resembling those of drier hummock locations. As previously noted, such change will result in an increase in the vulnerability, especially considering that lawns cover the largest area fraction of the peatland. Based on aerial photography and GPS measurements, we estimate that lawns cover about 69.6% of the 40 ha of *El Morro*, followed by 17.3% by hollows and 10.3% by hummocks.

Over the long-term (decades to centuries) effects on CH₄ flux and C sequestration are uncertain. First, prolonged dry conditions may lead to a major shift in vegetation composition, leading towards a marked dominance of graminoids and more likely increased CH₄ fluxes (Ward et al., 2013; Cao et al., 2017). However, a drastic water table draw-down over time may lead to the dominance of shrubs over graminoids (Weltzin et al., 2003; Benavides, 2014) and extended aeration of the soil. This change will reduce CH₄ fluxes while increasing CO₂ sink strength due to the interactive effects of shrub dominance at increased temperatures (Ward et al., 2013), but with an unknown increase in respiration and decomposition rates of now aerated organic soil. Second, despite a possible increase in CO₂ sink, water table draw-down can simultaneously increase peat subsidence by promoting decomposition (Potvin et al., 2015). In addition, water table draw-down can also increase peat decay and compaction which leads to higher fluctuations in water table providing a positive feedback to further peat decay (Whittington and Price, 2006). Moreover, peat decomposition will be exacerbated by losing labile carbon under warmer temperatures during dry periods (Ise et al., 2008).

It is harder to predict the trajectory of hollow locations as these are considerably lower in the microtopographic gradient, hence likely to maintain flooded, but may collapse with lowered water tables as the peat in the hollows is not well consolidated. Further studies should focus on the development of peatland formation models in the tropical Andean regions that can be used to properly assess the possible trajectories of peatland development under changing environmental conditions.

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